The effect of *Uni* on leaf shape

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The pleiotropic *unifoliata (uni;* 2,6) mutation reduces the complexity of the compound leaf. Leaves are tendril-less, ranging from unifoliate at lower nodes (including the scale leaves) to trifoliate at higher nodes prior to flowering. The uni^{tac} allele (7,8,10) has a similar, but weaker effect; the number of pairs of tendrils is reduced. Like *uni*, uni^{tac} mutants develop a leaflet at the terminal position. Both alleles are recessive, suggesting they may be loss-of-function variants. This implies that *Uni* functions to increase the complexity of the compound leaf.

Triple mutant combinations of the genes *afila* (*af*; 3,5), *tendril-less (tl;*1*)* and *uni,* were generated to test this inference and examine the effects of *Uni* on compound leaf structure. The leaves in Fig. 1 are from equivalent nodes and are homozygous for *af, tl* and *uni*, uni^{tac} or *Uni* from left to middle and right, respectively. Their arrangement shows the effect of incrementally adding *Uni* function to a pleiofila *(af/af, tl/tl)* leaf.

Two gradients of change are obvious. Firstly, the amount of branching increases from left to right, resulting in an increased number of leaflets. This demonstrates that *Uni* function does increase leaf complexity, as inferred from the *uni* mutant alleles. How does it do so? The adult leaves shown in Fig. 1 are the outcomes of earlier developmental events in the leaf primordia (4,9). The relative structural complexity of the *af/af, tl/tl, Uni/Uni* leaf (right) may be the passive result of *Uni* functioning in the leaf rachis meristem to maintain it in an indeterminate state (of unlimited growth potential; 11). Alternatively, *Uni* may have an active role, whereby its presence promotes the production of lateral primordia. Detection of the *Uni* transcript in developing leaf, rachide and leaflet primordia supports both these possibilities (J.Hofer, unpublished results).

Secondly, leaflet size decreases from left to right (Fig. 1). The surface area of individual laminae reflects the circumference of the rachis meristems from which they emerge. This gradient in leaflet size mimics, in an exaggerated way, the gradient in leaflet size from base to distal tip (left to right) of a single, homozygous *tl* leaf (Fig. 2). As it is known that the only changing factor in Fig. 1 is an increment in *Uni* function (from left to right), it is tempting to consider that the form of the leaf in Fig. 2 resulted from a temporal or physical gradient in *Uni* function that existed in the leaf rachis primordium.

Young (12) presented a model for pea leaf morphogenesis in which there were three possible meristem fates: rachis, leaflet or tendril, and the fate of a meristem was determined by its "size". In the model, "size" was an abstract notion, although it was clearly considered to be connected to physical dimension. The leaves shown here suggest that *Uni* function is somehow correlated with, or could substitute for, Young's "size".

Af, like *Uni,* regulates the complexity of the leaf, but is opposite in effect. Leaflets of the *af* mutant are replaced by branching rachides (Fig. 3; 3,5,12) indicating that *Af* functions to increase determinacy, or suppress the production of lateral primordia. *Uni* and *Af* can be likened to counterbalancing "accelerator" and "brake" signals in pea leaf development, *uni* leaves lack "acceleration", are unifoliate and resemble simple leaves, whereas *af* leaves lack

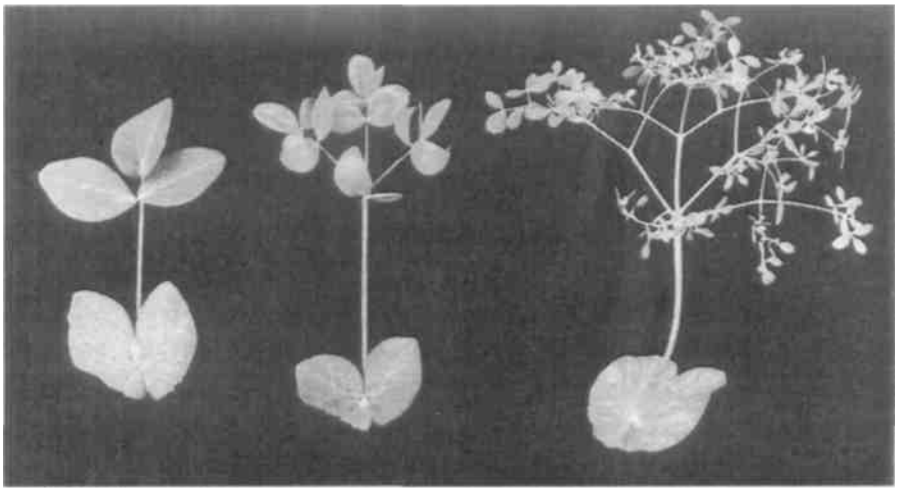

Fig. 1. Adult pea leaves from equivalent nodes: *af/af, tl/tl, uni/uni* (left), *af/af, tl/tl,* uni^{tac}/uni^{tac} (middle) and *af/af, tl/tl, Uni/Uni* (right).

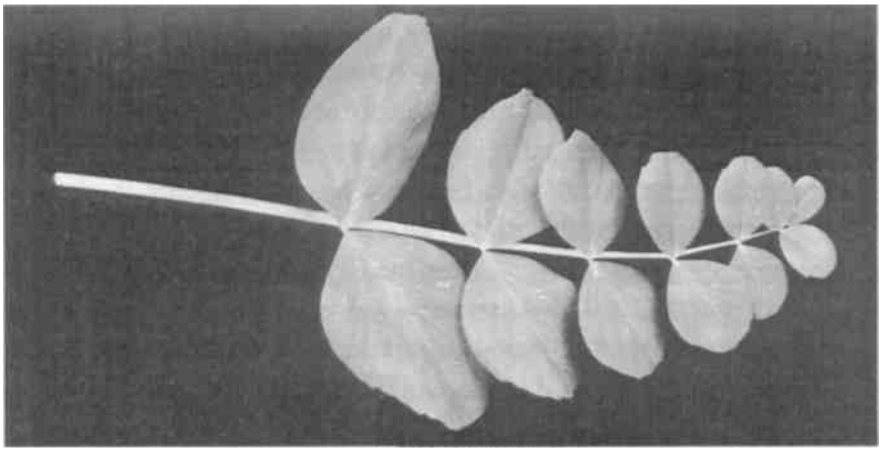

Fig. 2. Adult homozygous *tl/tl* leaf with stipules removed.

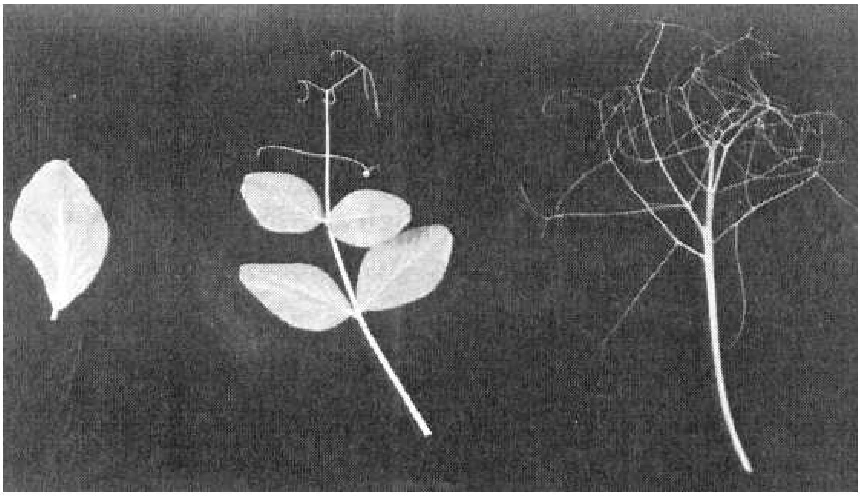

Fig. 3. Adult leaves with stipules removed: *uni/uni* (left), wild type (middle) and *af/af* (right).

"brakes" and appear supercompound, with multiple dividing rachides. The wild-type compound leaf results from a balance between these two opposing signals (Fig. 3).

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